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Lev Ryashko, Ivan Tsvetkov, and Bernardo Spagnolo

Noise-Induced Shifts in the Ecological Model with Delay

Lev Ryashko[1,a)], Ivan Tsvetkov[1,b)] and Bernardo Spagnolo[2,3,4,c)]

[1]*Department of Theoretical and Mathematical Physics, Ural Federal University, Lenina, 51, 620000, Ekaterinburg, Russia*
[2]*Department of Physics and Chemistry, Group of Interdisciplinary Theoretical Physics, Universitá degli Studi di Palermo and CNISM, Viale delle Scienze, Edificio 18, I-90128 Palermo, Italy*
[3]*Radiophysics Department, National Research Lobachevsky State University of Nizhni Novgorod, 23 Gagarin Avenue, Nizhni Novgorod 603950, Russia*
[4]*Istituto Nazionale di Fisica Nucleare, Sezione di Catania, Via S. Sofia 64, I-90123 Catania, Italy*

[a)]lev.ryashko@urfu.ru
[b)]itsvet@e1.ru
[c)]bernardo.spagnolo@unipa.it

Abstract. A Hassell-type mathematical model of population dynamics with delay and stochastic disturbances is considered. In this bistable model, one of the attractors corresponds to the extinction, and the other one describes non-trivial stable modes of dynamics. These modes can be both regular and chaotic. Structural stability zones are separated by local and global bifurcations. We study how noise shifts these bifurcation points and contracts the persistence zone. Abilities of the theoretical analysis of these phenomena with the help of the stochastic sensitivity function technique is discussed.

INTRODUCTION

A extinction of populations is one of the most important examples of ecological shifts. Dynamics of population systems depends on various factors, both internal and external. A mathematical analysis of mechanisms of the extinction is based on the bifurcation theory of nonlinear dynamical models with the complex regular and chaotic behavior [1, 2, 3, 4].

As any living systems, populations are subject to random disturbances which can cause noise-induced ecological shifts [5, 6, 7, 8, 9, 10] and result in the extinction. Our paper focuses of the study of the corporate influence of the Allee effect [11, 12], delay [13, 14], and random disturbances on the population dynamics. Mathematically, the Allee effect induces the multistability: the system possesses the nontrivial attractor corresponding to the persistense and the trivial equilibrium modeling the extinction. In these circumstances, the stochastic transition from the nontrivial attractor to the trivial one can be a reason of the noise-induced extinction [15, 16]. In this process, the delay complicates the analysis of these stochastic effects.

In our study, we use a conceptual Hassell-type population model [17] with the embedded Allee effect, delay, and stochasticity. An interplay of these factors is studied in the framework of the analysis of persistence zone. We show how this zone contracts under increasing noise. The theoretical approach based on the stochastic sensitivity function technique [18, 19, 20] and confidence domains method is discussed.

DETERMINISTIC MODEL

In the present paper, for the analysis of ecological shifts we will use the conceptual Hassell-type population model with the embedded Allee effect

$$x_{t+1} = \frac{x_t^{\alpha}}{(\beta + x_t)^6}. \tag{1}$$

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Here, x_t is a population density at the time t, and α is a positive parameter that describes a strength of the Allee effect. If $\alpha = 1$, there is no Allee effect in this system. In system (1), the positive parameter β models a carrying capacity of the environment. Here and further, we put $\alpha = 1.5$ and vary the parameter β.

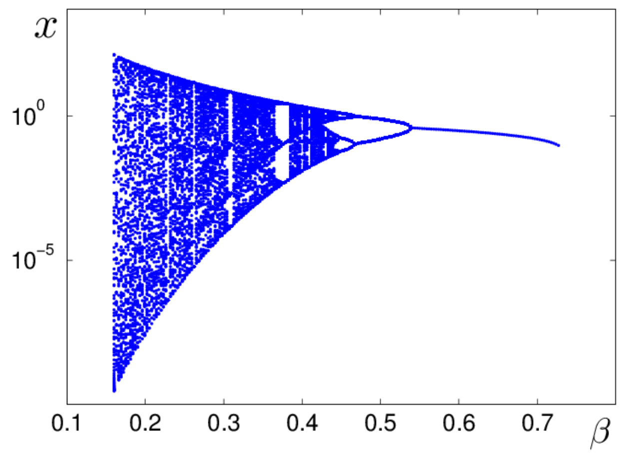

FIGURE 1. Nontrivial attractors of system (1) without delay.

For any $\beta > 0$, this system has the stable trivial equilibrium $\bar{x} = 0$. This equilibrium corresponds to the extinction of the population: for small initial densities x_0, due to Allee effect, the population size x_t tends to zero. In the interval $0.16 < \beta < 0.73$, system (1) is bistable. Along with the trivial equuilibrium, the system possesses nontrivial attractors (see Figure 1). In this β-interval, nontrivial attractors form the Feigenbaum tree with the regular or chaotic regimes. In the present paper, we focus on the modified version of system (1) which takes into account a dependence on the

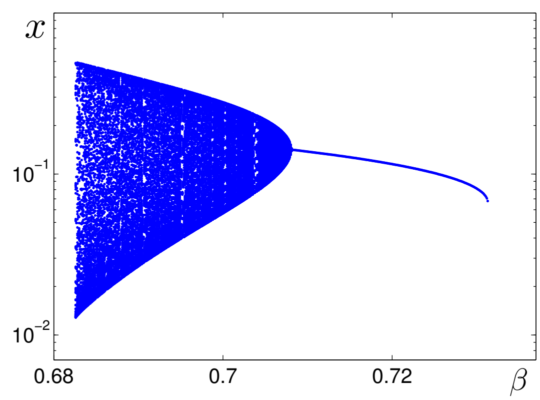

FIGURE 2. Nontrivial attractors of system (3).

previous generation:

$$x_{t+1} = \frac{x_t^\alpha}{(\beta + x_{t-1})^6}. \tag{2}$$

Let us rewrite the model (2) with delay as a two-dimensional system

$$\begin{aligned} x_{t+1} &= \frac{x_t^\alpha}{(\beta + y_t)^6} \\ y_{t+1} &= x_t. \end{aligned} \tag{3}$$

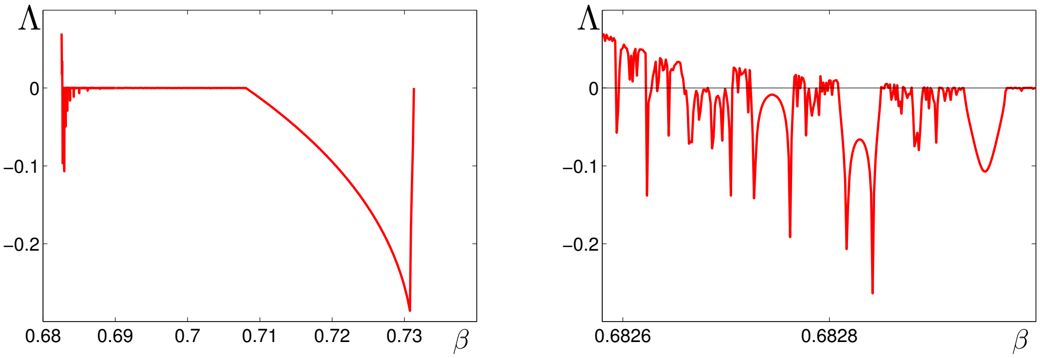

FIGURE 3. Largest Lyapunov exponents of nontrivial attractors of system (3).

Similar to system (1), the model (3) has the stable trivial equilibrium corresponding to the extinction. But nontrivial attractors exist on a significantly smaller interval $0.68258 < \beta < 0.73131$. In this β-interval, system (3) is bistable. Among all bifurcation values, we mark $\beta_1 = 0.68258$, $\beta_2 = 0.7082$, and $\beta_3 = 0.73131$. The point β_1 corresponds to the boundary crisis bifurcation, β_2 is the Neimark-Sacker bifurcation point, and β_3 is the saddle-node bifurcation point. In the framework of model (3), points β_1 and β_3 define borders of the persistence zone where the existence of the population is observed in various regimes. The internal point β_2 separates oscillatory and equilibrium regimes.

In Figure 2, x-coordinates of nontrivial attractors of system (3) are shown. In the interval $\beta_2 < \beta < \beta_3$, the system exhibits a stable equilibrium. In the interval $\beta_1 < \beta < \beta_2$, system (3) exhibits regular (periodic and quasiperiodic) and chaotic oscillations. In this interval, under decreasing β, the amplitude of oscillations increases.

In Figure 3, the plot of the largest Lyapunov exponent $\Lambda(\beta)$ of nontrivial attractors is shown. In the enlarged fragment, near β_1, one can see positive values of Λ that mark chaotic oscillations.

In Figures 4,5, some attractors from the persistence zone are shown. Here, for $\beta = 0.6826$, a chaotic attractor is plotted, for $\beta = 0.68295$ we have a discrete 19-cycle, for $\beta = 0.7$ and $\beta = 0.705$ one can see closed invariant curves corresponding to the quasiperiodic attractors. As one can see, in the persistence zone $\beta_1 < \beta < \beta_3$, system (3) demonstrates a rich variety of dynamical regimes. In the next Section, we will study how these dynamic regimes can be changed by random disturbances.

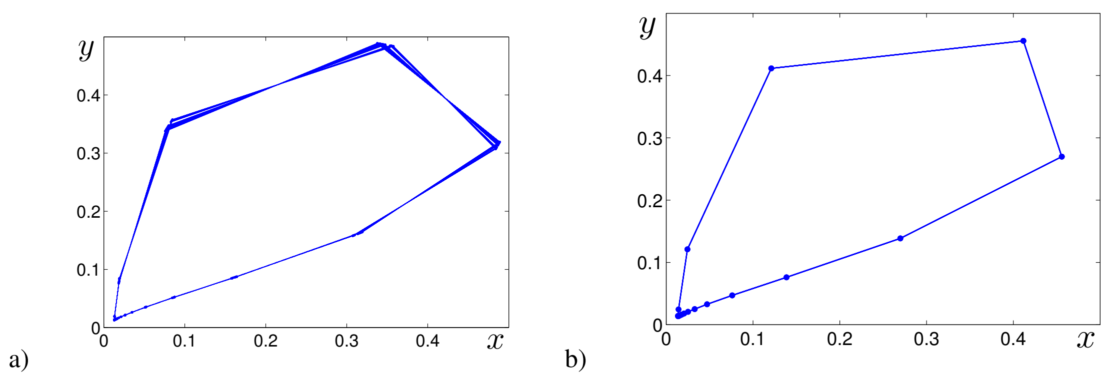

FIGURE 4. Attractors of system (3): a) chaos for $\beta = 0.6826$, b) 19-cycle for $\beta = 0.68295$

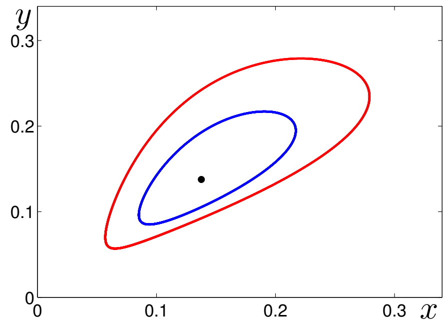

FIGURE 5. Attractors of system (2): closed invariant curves for $\beta = 0.7$ (red), $\beta = 0.705$ (blue) and equilibrium for $\beta = 0.71$.

NOISE-INDUCED EXTINCTION IN STOCHASTIC POPULATION MODEL

Consider the Hassell-type model (2) with delay in presence of multiplicative random disturbances

$$x_{t+1} = \frac{x_t^{\alpha}}{(\beta + x_{t-1})^6} + \varepsilon x_t \xi_t. \tag{4}$$

Here, ξ_t is a standard uncorrelated scalar random process with parameters $\mathrm{E}(\xi_t) = 0, \mathrm{E}(\xi_t^2) = 1$, and ε is an intensity of the environmental noise.

Rewrite this stochastic model in the following form

$$\begin{aligned} x_{t+1} &= \frac{x_t^{\alpha}}{(\beta + y_t)^6} + \varepsilon x_t \xi_t \\ y_{t+1} &= x_t. \end{aligned} \tag{5}$$

For any β from the persistence interval, the deterministic system (3) has a non-trivial attractor. In our numerical simulations, we calculate random solutions of system (5) starting from these deterministic attractors. For small noise intensity, random states are slightly dispersed near the initial unforced deterministic attractors. As noise intensity increases, the dispersion grows, and random trajectories can exit the basin of attraction of the initial non-trivial attractor. If these trajectories fall into the basin of attraction of trivial equilibrium, the population becomes extinct.

In Figure 6, for $\beta = 0.7$, we consider a case when the deterministic system (3) has a closed invariant curve as the nontrivial attractor (blue). It is shown how the phase random trajectory (red) of system (5) with $\varepsilon = 0.1$ leaves this deterministic attractor and after a couple of turns starts to tend to the origin. This is an example of the noise-induced extinction. Corresponding time series are shown on the right.

In Figure 7, for $\beta = 0.73$, we show how the noise-induced extinction occurs in the equilibrium regime. Here, the nontrivial equilibrium is shown by blue color. For small noise with $\varepsilon = 0.01$, random trajectories (green) leave this equilibrium and locate nearby. For stronger noise with $\varepsilon = 0.1$, the stochastic trajectory (red) moves from the nontrivial equilibrium and tends to the origin. So, the population system becomes extinct.

Details of such noise-induced ecological shifts in dependence on the parameter β from the persistence zone are shown in Figures 8, 9. In Figure 8, we consider three values of β corresponding to the oscillatory regimes. With increasing noise, one can see a gradual increase of the amplitude of oscillations. This increase is abruptly interrupted by the extinction. The threshold noise intensity which corresponds the onset of the extinction essentially depends on the parameter β: the closer β to the crisis bifurcation value β_1, the smaller the threshold noise intensity. In Figure 9, we consider a mechanism of the noise-induced extinction in the equilibrium zone. Here, the threshold noise intensity decreases as β approaches the bifurcation value β_3.

So, noise contracts the persistence zone. This fact can be clearly seen also in Figure 10. Here, mean values $m(\beta)$ of random states $x_t,\ t = 0, 1, \ldots N,\ N = 5 \cdot 10^3$ are shown for various noise intensities.

Note that parts close to the left and right borders of the persistence zone are more sensitive to noise. In these parts, even weak noise transforms the system to extinction. The value $\beta \approx 0.714$ corresponds to the most resistance to noise.

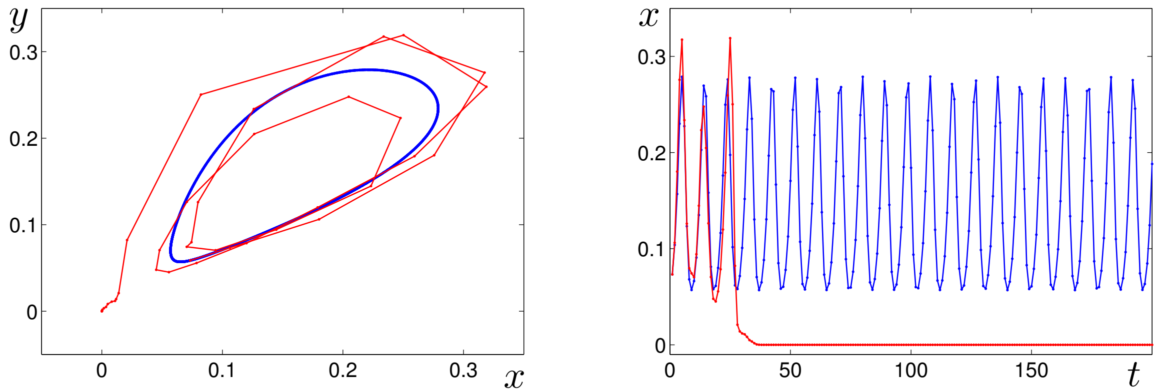

FIGURE 6. Noise-induced extinction in stochastic system (5) for $\beta = 0.7$ and $\varepsilon = 0$ (blue), $\varepsilon = 0.1$ (red).

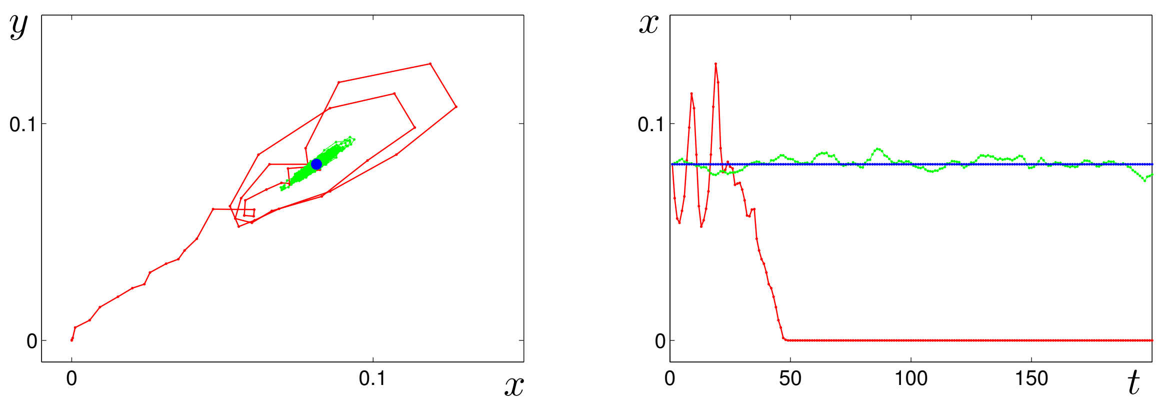

FIGURE 7. Noise-induced extinction in stochastic system (3) for $\beta = 0.73$ and $\varepsilon = 0$ (blue), $\varepsilon = 0.01$ (green), $\varepsilon = 0.1$ (red).

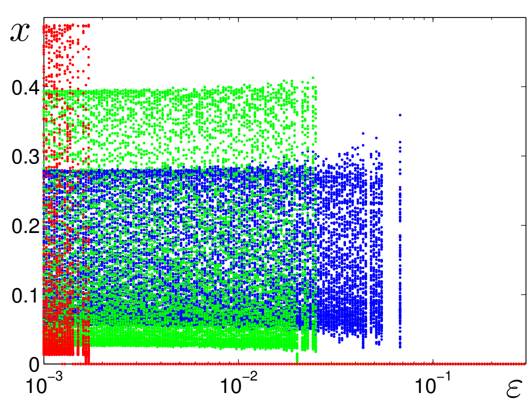

FIGURE 8. Noise-induced extinction in stochastic system (3) for $\beta = 0.7$ (blue), $\beta = 0.69$ (green), $\beta = 0.683$ (red).

Biologically, this value marks the optimal size of the ecological niche for which the population system preserves the persistence for the highest possible noise level.

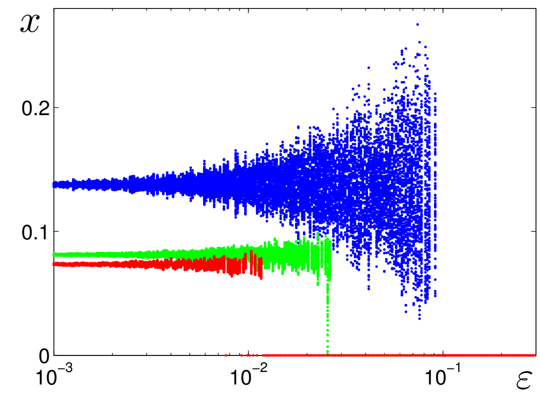

FIGURE 9. Noise-induced extinction in stochastic system (3) for β = 0.71 (blue), β = 0.73 (green), β = 0.731 (red).

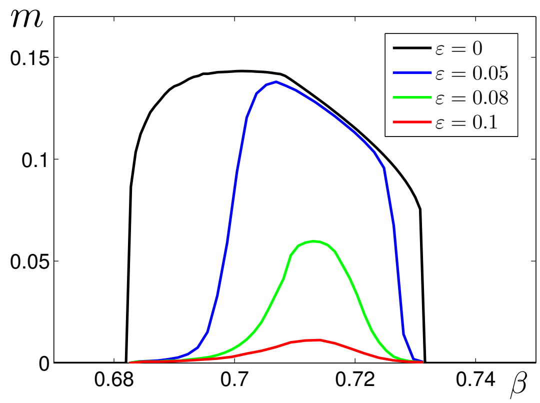

FIGURE 10. Noise-induced contraction of the persistence zones for stochastic system (3) with γ = 1.5: mean values m of x-coordinates.

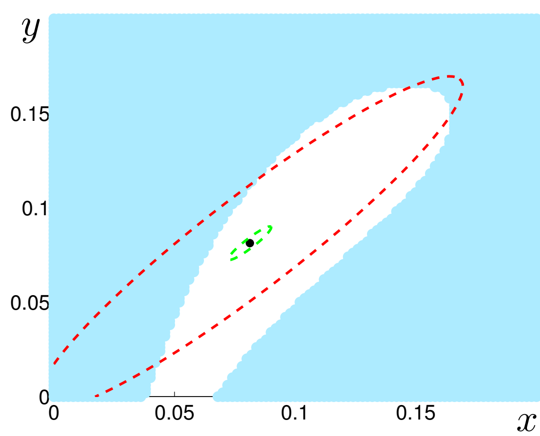

FIGURE 11. Confidence ellipses for stochastic system (3) with β = 0.73 and ε = 0.01 (green), ε = 0.1 (red).

To analyse the noise-induced extinction one can use the stochastic sensitivity function technique [16, 21, 22]. In Figure 11, confidence ellipses constructed on the base of the stochastic sensitivity function technique are plotted for $\beta = 0.73$ and $\varepsilon = 0.01$ (green), $\varepsilon = 0.1$ (red). The basin of attraction of the trivial equilibrium is shown in light blue. As can be seen, the small ellipse with $\varepsilon = 0.01$ entirely belongs to the basin of attraction of the nontrivial equilibrium. For $\varepsilon = 0.1$, the ellipse partially occupies the basin of attraction of the trivial equilibrium. This means the onset of the noise-induced of the noise-induced extinction (compare with Figure 7).

Conclusion

We studied a phenomenon of the noise-induced extinction on the base of the conceptual Hassell-type population model with delay and random forcing. Mathematically, this phenomenon can be investigated by means of stochastic transitions from non-trivial attractor to the trivial one. It was shown that borders of the persistence zone are defined by the saddle-node and crisis bifurcations. By the direct numerical simulations, we studied how noise shifts these borders and contracts the persistence zone. It should be noted that in the theoretical analysis of the noise-induced contraction of the persistence zone the stochastic sensitivity function technique can be used. In the framework of this approach, the noise-induced extinction was studied by the geometrical analysis of the mutual arrangement of basins of attraction of coexisting attractors and confidence ellipses.

Acknowledgments

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